

WHY DO SOME COMPOSITAE HAVE AN INCONSISTENTLY DECIDUOUS PAPPUS?¹

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Many species of Compositae produce seeds equipped with a pappus that acts as a parachute, allowing the seeds to be dispersed by wind (Zohary, 1937, 1950; Pijl, 1972; Burtt, 1961, 1977). Surprisingly, in some other species the pappus is formed but deciduous, i.e., separates very easily from the body of the seeds, usually before dispersal. This trait seems paradoxical—why manufacture a dispersal apparatus and then drop it before dispersal? To our knowledge, no adaptive value for deciduousness has been put forward in the literature. Nonetheless, deciduousness is a common phenomenon recorded in Compositae from virtually all tribes, regions, and habitats.

As an initial stage in investigating possible adaptive values of a deciduous pappus, I have analyzed the Compositae in the flora of Israel for correlations between deciduousness and other ecological parameters. The results of this survey, which I present here, suggest that inconsistent deciduousness is adaptive primarily as a mechanism for achieving a mixed dispersal strategy, in which seeds that lose their pappus prior to dispersal remain in the vicinity of the mother plant (“atelechory” sensu Ellner & Shmida, 1981).

The analysis is based on Feinbrun-Dothan (1978) supplemented by extensive observations of species distributions and seed characters in Israel. Several species which have been found only sporadically in Israel, and appear not to be established in the flora, were excluded from the analysis. Seeds bearing only a few pales or awns, or a corolla, were regarded as epappose. Copies of the species-list with scorings for all attributes used in the analysis are available on request.

Associations between deciduousness and other attributes were examined by constructing 2×2 contingency tables in which the rows were defined by deciduousness versus persistence of the pappus, and the columns by presence versus absence of the other attribute. The tables were tested for significance at the level $\alpha = 0.05$ by either the chi-square test or (if any of the expected cell

counts were ≤ 5) the exact multinomial test for a 2×2 table.

Of the 230 Compositae found in Israel, 42 have a deciduous pappus (DP), 112 have a persistent pappus, and the remainder are epappose. About half (22) of the species with a deciduous pappus are annuals. However, no significant associations were found between DP and growth-form (annual, biennial, perennial) or life-form (annual, hemicriptophyte, chamaephyte) in the Mediterranean region, the desert region, or both regions combined. I also investigated possible associations between DP and the following special habitats: Mediterranean region, desert region, rock outcrops, hygrophile and ruderal. A significant positive association was found between DP and ruderal habitats (Table 1a) (because all but two ruderals were classed as Mediterranean, only Mediterranean species were considered). However, this association appears to be an artificial consequence of two other associations: a strong negative association between DP and pappus dimorphism (Table 2), and a negative association between pappus dimorphism and ruderal habitats (Table 1b). If I remove this confusing trend by excluding species with a pappus dimorphism, there remains a positive but highly non-significant association between DP and ruderal habitats (Table 1c).

Thus, the only significant trend is that DP generally does not occur in species with pappus dimorphism. The term dimorphic pappus is used here in any case in which the achene of the same capitulum has more than one morphological type of pappus. The transition between type of pappus in the capitulum can be abrupt or gradual. The present article does not analyze heteromorphic achene, a phenomena which is correlated with heteromorphic pappus (Ellner & Shmida, 1981; Shmida & Ellner, in prep.). In the Compositae of Israel, pappus dimorphisms almost invariably involve a substantial reduction or complete elimination of the pappus on a portion of the achenes

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TABLE 1. Deciduous pappus and pappus dimorphism in relation to ruderal habitats in the Mediterranean region Compositae of Israel (cell entries are numbers of species).

	Ru- deral	Non-ru- deral
(a) Deciduous pappus ^a	16	15
Persistent pappus	20	52
(b) Pappus dimorphism present ^a	3	27
Pappus dimorphism absent	23	40
(c) Species without pappus dimorphism ^a		
Deciduous pappus	16	14
Persistent pappus	17	26

^a The 2×2 tables in (a) and (b) (involving all Mediterranean region Compositae) depart significantly from independence ($\chi^2 = 4.42$ and 5.84 , $P < 0.05$ and $P < 0.025$ respectively). The table in (c) (Mediterranean Compositae without a pappus dimorphism) does not depart significantly from independence ($\chi^2 = 0.86$, $P > 0.25$).

in each capitulum. DP and pappus dimorphism can therefore be viewed as alternative mechanisms which reduce the efficacy of wind-dispersal in some (but not all) seeds. The finding is that species tend not to utilize both alternatives. This is illustrated nicely in the genus *Crepis*: of the 12 species found in Israel, six have a deciduous monomorphic pappus, and six have a persistent pappus with a marked pappus dimorphism between marginal and central seeds in a capitulum (Feinbrun-Dothan, 1978). Similarly, in the *Filago* group (sensu Wagenitz, 1969; Feinbrun-Dothan, 1970), *Cymbolaena* and *Lasiopogon* spp. in Israel have a deciduous, monomorphic pappus, while in *Filago* and *Ifloga*, the central fertile achene in each capitulum has a persistent pappus and the marginal seeds are epappose (Feinbrun-Dothan, 1978).

These results suggest that DP and pappus dimorphism are alternative means to some end, but give no clue as to what that end might be. The most obvious conjecture has to do with seed dispersal distance. A pappus classed as "deciduous" may separate from the seed either before or after dispersal. My observations of *Lactuca* spp., *Carduus* spp., *Onopordon* spp., *Silybum marianum*, *Urospermum picroidis*, and *Notobasis syraica* indicate that some of the seeds produced by an individual lose their pappus before dispersal, while others lose their pappus only upon impact after dispersal.

TABLE 2. Deciduous pappus in relation to pappus dimorphism in the Compositae of Israel (cell entries are numbers of species).

	Medi- terra- nean Region ^a	Desert Region ^a	Entire Flora
Pappus dimorphism present ^b			
Deciduous pappus	2	2	4
Persistent pappus	14	24	38
Pappus dimorphism absent			
Deciduous pappus	14	25	38
Persistent pappus	32	46	74

^a Five species found in both Mediterranean and desert regions are recorded in each.

^b The paucity of dispersal-heterocarpic species with deciduous pappus is significant at $\alpha = 0.05$ in each region and in the entire flora (exact test for a 2×2 table applied to each column individually).

DP and pappus dimorphism thus both result in a partial loss of "long-distance" dispersal by wind. Mixed dispersal strategies, in which some seeds disperse while others remain near the parent plant, have been found to be optimal in various models of species in spatiotemporally variable environments (Hamilton & May, 1977; Comins et al., 1980; Motro, 1982a, 1982b; Levin et al., 1983) and also in spatially structured but temporally constant environments (Hamilton & May, 1977; Motro, 1982a, 1982b). In patchy, variable habitats, dispersal allows a species to colonize suitable patches. Exploitation of suitable patches by subsequent generation requires retention of some seeds in the patch. Partial dispersal achieves both these ends, and a partial dispersal strategy is therefore generally optimal (Shmida & Ellner, 1984).

Other adaptive values for the lack of a pappus can also be conjectured. For example, epappose seeds may enter more readily into small cracks or openings in the soil, and buried seeds may avoid predation and thermal extremes faced by seeds lying at the soil surface (Ellner & Shmida, 1981). Conversely, epappose seeds are smaller and presumably easier for insect predators to handle.

The question remains, why produce a pappus if it is advantageous to lose it? Why not reduce or eliminate the pappus on some seeds? I hypothesize that the reason is evolutionary flexibility. A pappus "lost" by deciduousness can be regained by strengthening the attachment of pap-

pus to seed, a minor modification compared to redeveloping the entire pappus. However, the contemporary suggestion that a deciduous pappus can easily be reconverted to a functional condition (= high evolutionary flexibility) should be demonstrated experimentally in the future. The fraction of wind-dispersed seeds can therefore vary over ecological time. This feature would be most valuable in patchy, variable habitats where newly-created patches remain suitable for extensive periods, during which time non-dispersal would be favored, a hypothesis which should be tested in the future. When a patch starts to become unsuitable, dispersal would be favored.

Preliminary observations in the field with the Israeli Compositae flora indicate much variation within the dispersal dynamic of species with an inconsistently deciduous pappus:

a) The pappus can break before or after dispersal and the percentage of pre-dispersal breakage versus post-dispersal breakage changes within a capitulum, within a population.

b) Within the obligatory deciduous species known from the systematic literature, at least in some species, there is prominent variation in the field in the percentage of the capitulum's achenes which dispersed with or without a pappus. We hypothesize that such variation can serve as a dynamic mechanism of evolutionary flexibility toward selection (and reversed selection) of an adaptive phenomenon of a deciduous pappus on the whole, as well as the adaptability of an inconsistently deciduous pappus.

The large, spiny ruderals with deciduous pappi found on anthropogenic mounds of nitrogen-rich soil (species of *Carduus*, *Silybum*, *Notobasis*, *Cynara*, and *Onopordon*) may be an example of this syndrome. New mounds are constantly being created, and persist for several years. Populations of *Silybum marianum* and *Onopordon cynarocephalum* in different localities vary markedly in the fraction of seeds losing the pappus prior to dispersal (70–100% in ten populations of *Silybum*, 60–100% in three populations of *Onopordon*), possibly representing different phases

in the cyclic selection for dispersal and non-dispersal, a hypothesis that should be tested.

LITERATURE CITED

- BURTT, B. L. 1961. Compositae and the study of functional evolution. *Trans. & Proc. Bot. Soc. Edinburgh* 39: 216–232.
- . 1977. Aspects of diversification in the capitulum. Pp. 41–59 in V. H. Heywood, J. B. Harborne & B. L. Turner (editors), *The Biology and Chemistry of the Compositae*. Academic Press, London and New York.
- COMINS, N. H., W. D. HAMILTON & R. M. MAY. 1980. Evolutionary stable dispersal strategies. *J. Theor. Biol.* 82: 205–230.
- ELLNER, S. & A. SHMIDA. 1981. Why are adaptations for long-range seed dispersal rare in desert plants? *Oecologia* 51: 133–144.
- FEINBRUN-DOTHAN, N. 1970. A key to the species of *Filago* L. sensu lato (Compositae) in Palestine. *Israel J. Bot.* 19: 260–265.
- . 1978. *Flora Palaestina*. Part 3: Ericaceae to Compositae. Israel Academy of Science and Humanities, Jerusalem.
- HAMILTON, W. D. & R. M. MAY. 1977. Dispersal in stable habitats. *Nature* 269: 578–581.
- LEVIN, S. A., D. COHEN & A. HASTINGS. 1983. Dispersal strategies in patchy environments. *Theor. Pop. Biol.* (in press).
- MOTRO, U. 1982a. Optimal rates of dispersal. 1. Haploid populations. *Theor. Pop. Biol.* 21: 394–411.
- . 1982b. Optimal rates of dispersal. 2. Diploid populations. *Theor. Pop. Biol.* 21: 412–429.
- PIJL, L. VAN DER. 1972. *Principles of Dispersal in Higher Plants*. Springer Verlag, New York.
- SHMIDA, A. & S. ELLNER. 1984. Coexistence of plant species with similar niches. *Vegetatio* 58: 29–55.
- VENABLE, D. L. & L. LAWLOR. 1980. Delayed germination and dispersal in desert annuals—escape in space and time. *Oecologia* 46: 272–282.
- WAGENITZ, G. 1969. Abgrenzung und Gliederung der Gattung *Filago* L. s.l. (Compositae-Imuleae). *Willdenowia* 5: 395–444.
- WHITTAKER, R. H. & S. A. LEVIN. 1977. The role of mosaic phenomena in natural communities. *Theor. Pop. Biol.* 12: 117–139.
- ZOHARY, M. 1937. Die Verbreitungsoekologischen Verhaeltmisse der Pflanzen Palaestinas. *Beih. Bot. Centralbl.* 61A: 1–155.
- . 1950. Evolutionary trends in the fruiting head of Compositae. *Evolution* 4: 103–109.